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Global and local threats to coral reef functioning and existence: review and predictions

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Abstract. Factors causing global degradation of coral reefs are examined briefly as a basis for predicting the likely consequences of increases in these factors. The earlier consensus was that widespread but localized damage from natural factors such as storms, and direct anthropogenic effects such as increased sedimentation, pollution and exploitation, posed the largest immediate threat to coral reefs. Now truly global factors associated with accelerating Global Climate Change are either damaging coral reefs or have the potential to inflict greater damage in the immediate future: e.g. increases in coral bleaching and mortality, and reductions in coral calcification due to changes in sea-water chemistry with increasing carbon dioxide concentrations. Rises in sea level will probably disrupt human communities and their cultures by making coral cays uninhabitable, whereas coral reefs will sustain minimal damage from the rise in sea level. The short-term (decades) prognosis is indeed grim, with major reductions almost certain in the extent and biodiversity of coral reefs, and severe disruptions to cultures and economies dependent on reef resources. The long-term (centuries to millennia) prognosis is more encouraging because coral reefs have remarkable resilience to severe disruption and will probably show this resilience in the future when climate changes either stabilize or reverse.

Introduction

It has become patently clear that coral reefs around the world are coming under increasing pressures and their status is declining rapidly. Calls for action on the effects of anthropogenic damage increased during the late 1980s and came to a head in 1992 and 1993 when two major events focussed on reef decline. The two plenary addresses at the 1992 7th International Coral Reef Symposium in Guam discussed the declining status of reefs (Buddemeier 1993; Wilkinson 1993). This was the strongest emphasis put on applied and management aspects of reefs at these, essentially scientific, symposia. In 1993, a special conference convened in Miami to document reef decline alarmed participants with a succession of reports of degradation from all parts of the world (Ginsburg 1993). The alarm was repeated with the Reefs at Risk analysis (Bryant *et al.* 1998) and then with the predictions in this issue by Hoegh-Guldberg (1999).

Probably as a result of such alarm calls, governments around the world launched the International Coral Reef Initiative in 1994 (Crosby *et al.* 1995), which spelt out definitive calls for international action in 1995 and 1998 (International Coral Reef Initiative, Anon. 1995, 1999). Soon afterwards, the Government of the USA launched a major task force for the conservation and sustainable management of coral reefs in their sphere of influence (Clinton 1998).

A key issue in this discussion is the time scale. Most scientists working on reefs fall into two broad categories: those focussing on geological time scales (10^2 to 10^8 years); and those working at biological scales of seconds to decades (10^{-6} to 10^1 years). Coral reefs have existed as something resembling the present form since the Mesozoic (~200 million years ago), surviving major environmental events such as massive falls in sea level during glaciation periods, meteor strikes, and large changes in solar activity (Veron 1986). Coral reefs recovered after these events to form extensive reefs with high biodiversity; however, recovery probably occurred over thousands to hundreds-of-thousands of years (10^3–10^6 years). The present 'human' time scales for considering reef recovery are those experienced after catastrophic tropical storms, plagues of the crown-of-thorns starfish *Acanthaster planci*, and previous bouts of severe, but localized coral bleaching. Reef 'recovery' to similar levels of coral cover occurred over periods of 15–30 years, with some reefs taking up to 100 years (Done 1999). However, the recovered reef could differ considerably in species composition, biological assemblages and reef-building capacity from the original (Done 1999).

Up to early 1998, direct anthropogenic stresses were regarded as the major threat to coral reefs (Salvat 1992; Wilkinson 1993; Bryant *et al.* 1998). Indeed, a specific review by a global task team looking for potential effects of climate change virtually ruled out effects of Global Climate Change in the following decades (Wilkinson and Buddemeier 1994). The major influences considered were increased sediment loading, organic and inorganic pollution and over-exploitation, which are seen as diminishing circles of impact spreading away from centres of human population (e.g. the predictive maps in Bryant *et al.* 1998). These changes were damaging coral reefs and the threats were increasing proportionally with both population and economic growth.

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The damage from these direct anthropogenic effects was localized, such that large areas of remote coral reefs (42% in Bryant *et al*. 1998) were unaffected. The growing exception was over-exploitation by roving bands of fishermen, which were systematically targeting reefs in widening concentric circles out from the major importing markets of East Asia (Hodgson 1999).

The basis for discussion on coral reefs switched radically in 1997–98, when truly global threats to coral reefs were added to the combination of damaging local factors (Buddemeier 1999). The critical change was that remote, previously 'pristine' reefs were being severely damaged. First, there was unprecedented coral bleaching and mortality in large parts of the world (Wilkinson 1998; Hoegh-Guldberg 1999), particularly in remote parts of the Indian Ocean (Wilkinson *et al*. 1999; Sheppard 1999). Then the latent fears of chemical imbalances in the sea water following increased dissolved CO_2 concentrations were illustrated in a model showing that reefs would be under increased threats in the future (Kleypas *et al*. 1999).

This review is not all encompassing, but focusses on the past decade, drawing heavily on recent papers and reviews (Buddemeier and Smith 1988; Wilkinson and Buddemeier 1994; Birkeland 1997; Brown 1997; Done 1999; Hoegh-Guldberg 1999). The major effect of Global Climate Change —increasing temperatures leading to coral bleaching and mortality—is covered in Hoegh-Guldberg (1999), which includes discussion of the associated impact of increasing concentrations of CO_2 reducing coral calcification (Kleypas *et al.* 1999). The main purpose here is to attempt predictions of the probable consequences of direct and indirect anthropogenic factors that are increasing as human populations and economic activity increases.

Coral reef variability and gradients

The major problems in assessing the status of reefs and attempting predictions of their future status are: *(1)* defining a coral reef and putting limits on the definition; and *(2)* determining where they are and what is the total area covered. There is no universally accepted definition of a coral reef. The working definition used here is: a coral reef is a complex marine ecosystem of animals, plants and minerals in which most of the basal and vertical structures have been and are being constructed with calcium carbonate secreted by hermatypic corals and coralline algae, along with a variety of other carbonate- and silicate-secreting organisms.

A coral reef generally falls within one of the following broad categories: fringing, platform, barrier, bank and atoll (Fig. 1). An important component of the definition is that coral reefs contain the highest biological diversity of any marine ecosystem and certainly a higher content of Phyla (30 of 34 recorded, Paulay 1997) than the oft-repeated comparison, tropical rain forests (Norris 1993).

Estimations of areal coverage of reefs vary greatly depending on the methods used and the definition of reef included: the first was a probabilistic calculation by Smith (1978) of 617 000 km^2. Similarly, Kleypas (1997) estimated reef area at between 584 000 and 746 000 km^2 growing down to 40 m, and up to 3 930 000 km^2 if all areas of shallow water to 150 m were included in the model equations. Another estimate, of

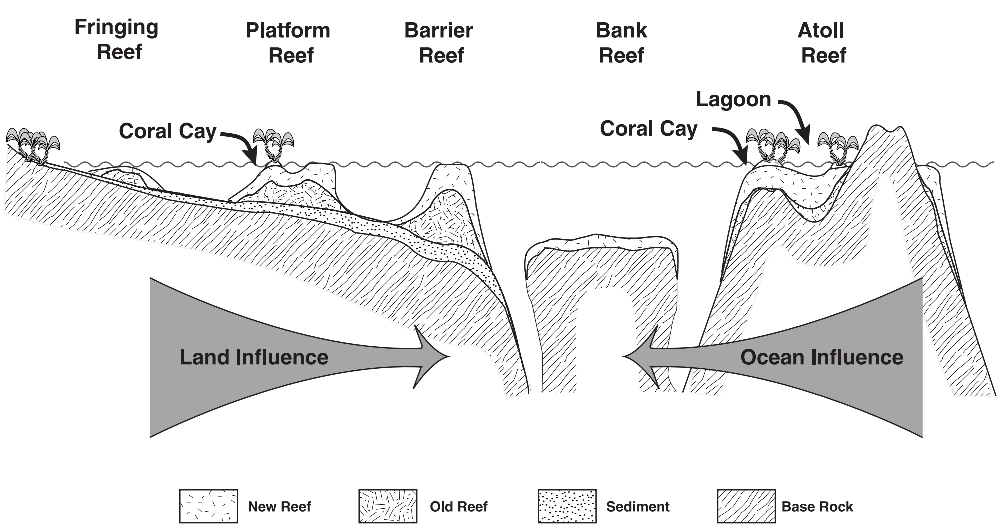

Fig. 1. The five major coral reef types of the world, showing the extent of terrestrial influence (sediment, fresh water, nutrients including pollution, and the origin of most fisheries exploitation) affecting principally fringing reefs, often platform reefs close to land or on shallow continental shelves, and some barrier reefs, particularly on the inner margins. By contrast, the ocean influence is almost the reverse: clean, low-nutrient waters, strong turbulence and larvae from distant reefs, with the largest effects on the oceanic atoll and bank reefs. The area covered by bank reefs in the world is largely unknown, whereas there are reasonable estimates of the other categories, which are visible in aerial and satellite images.

1 500 000 km^2, was made by adding carbonate banks and 'dead' reefs to the Smith estimate of coral reef area (Copper 1994). A more restricted estimation was 225 000 km^2, which focussed on known shallow-water reefs but recognized that there are probably larger areas of bank reefs (Spalding and Grenfell 1997). In general, coral reefs form in waters at temperatures at or above 20°C throughout most of the year and with relatively even day length. Thus, most coral reefs are found between 25° Latitude north and south of the Equator.

There is considerable variability among reefs (Fig. 1), the organisms that live on different reefs, and individual organisms within a single reef, e.g. among different species of corals and other biota, or even within a single species (Fig. 2). This is critical because observations or research on one reef or on a few species will rarely apply to other reefs and certainly not to all reefs world-wide. There has been an unfortunate tendency to apply results of limited experiments to global conclusions. Below are listed some of the parameters that vary across coral reef locations and affect the distribution of species (Fig. 2). These observations specifically refer to reef-building corals, but often are applicable for many other organisms on coral reefs, and are listed because they influence the predictions that follow.

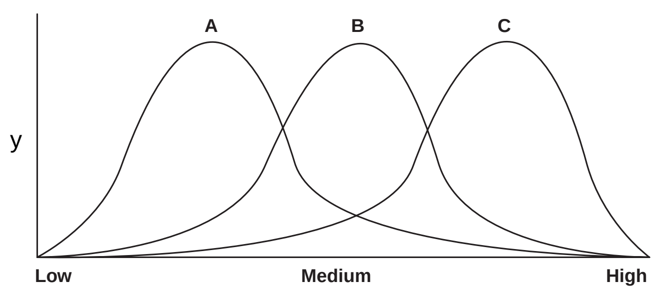

Fig. 2. A series of three hypothetical 'normal' distribution curves for coral reef animals showing population sizes or species numbers on the Y axis against 'environment', e.g. sediment or nutrient or pollution concentration, temperature variability, salinity, along the X axis. Most reef populations are regarded as being of curve type B; however, reefs close to land contain a higher content of species able to exist in high sediment or higher nutrient habitats e.g. curve C, as opposed to oceanic reefs, which will have a distribution resembling curve A. Similarly, where temperatures are more variable (shallow reef flats, enclosed bays, and larger enclosed areas such as the Arabian Gulf) coral populations have a higher proportion of species able to resist higher levels of temperature variability (curve C), than oceanic reefs in more thermally stable environments (curve A).

Latitude

True coral reefs occur from about 31° (southern Japan) and 32° (Bermuda) north, and 29° (Houtman Abrolhos reefs off western Australia) and 32° (Lord Howe off eastern Australia) south of the Equator. The critical factors limiting growth at latitudes outside ~25°N and 25°S are temperature and/or day length. All the reefs above are influenced by warm currents flowing towards the poles. The Kuroshio Current off Japan carries corals as far north as 35°N, near Tokyo; the Gulf Stream allows the Bermuda reefs to grow ~600 km north of the Bahamas; the Leewin Current warms the Abrolhos reefs off Western Australia; and the East Australia Current permits reefs to grow around Lord Howe Island. These currents bring both warm water, which replaces the cooler ambient temperatures, and new coral reef larvae to repopulate these reefs when they are occasionally affected by low-temperature stresses that kill corals and other organisms. The other major factor that limits polewards growth of reefs is the decreasing day length for hermatypic corals. During mid winter, corals in high latitudes receive little photosynthetically active radiation (PAR) because ambient solar radiation energy is weak, low sun angle results in considerable reflectance off the surface with little penetration into the water, and day length is short (see Depth, below). These factors do and will continue to limit the spread of reefs polewards with increasing sea surface temperatures.

Depth

Reef-forming corals frequently grow from the surface to 50–60 m depths on reefs in mid-oceanic waters where there is adequate available light. Some corals have been dredged from as deep as 100 m (Veron 1986). As for high latitudes, the limiting factor for corals is predominantly the available PAR, which is attenuated progressively with depth through absorption in the water, accentuated by particles in the water. Corals are capable of considerable photoadaptation through changes in morphology, respiration rates, chlorophyll content of symbiotic algae and greater emphasis on heterotrophy (Chalker *et al.* 1983; Porter *et al*. 1984; Wilkinson 1986), but such adaptation has definite limits. Another critical factor of depth is the surrounding sea floor. Reefs on shallow continental shelves experience a greater influence from the land, with sediments and nutrients resuspended by movements of the overlying waters, and they generally do not grow below 20–30 m depth (Fig. 1), whereas reefs in oceanic waters can grow down to 100 m (Intes and Caillart 1994).

Temperature

The generally accepted range is 18–36°C, with the optimal temperature between 22° and 28°C (Hubbard 1997). Although few reefs ever experience this total range, there are some in the Persian Gulf that experience temperatures well outside the upper and lower ends of this range (11–36°C) and still 'survive' (Coles 1997). However, most corals exist near their upper thermal limits in summer, and rises in temperature above this frequently lead to coral bleaching (Glynn 1996); whereas large falls in temperature have few effects. The topic of temperature is discussed in more detail by Hoegh-Guldberg (1999).

A critical factor in survival after increased temperatures is the degree of thermal acclimatization developed by corals before temperatures rise. Corals that normally experience wide fluctuations in temperature, such as those on reef-flats, survive much better (Fig 2; Hoegh-Guldberg and Salvat 1995; Augustin *et al.* 1997). This was evident in Palau after the 1998 bleaching; the outer reefs were severely affected, with almost total elimination of live corals, whereas reef-flat corals and those growing on more temperature-variable inshore environments showed a far greater survival (Paulay, Richmond and Birkeland, personal communication).

Salinity

The optimal range of salinity is 32–40 (Veron 1986); however, there are coral species that can grow across a wide gradient of salinities from 40 up to 55 in the Arabian Gulf (George and John 1999) and down to as low as 20 for limited periods in semi-enclosed bays following freshwater input. There is probably no single coral species that can withstand this full range, but some species and genetic strains will be more tolerant than others. Again, it is the rate of change, rather than the specific level of salinity, that has deleterious effects on corals.

Nutrient levels

The statement that coral reefs are oases of biodiversity in oceanic deserts is frequently true, especially for mid-oceanic reefs where the concentration of inorganic nutrients is particularly low. This in turn leads to low amounts of circulating organic carbon, such that these corals are predominantly phototrophic (dependent on photosynthesis for most of their nutrition; Muller-Parker and D'Elia 1997). However, many coral species are quite capable of growing in waters with much higher concentrations of inorganic and organic nutrients using heterotrophic feeding; e.g. Veron (1986) showed that some of the highest coral diversity on the Great Barrier Reef occurred within a few kilometres of significant rivers on inner-shelf reefs with elevated levels of nutrients and suspended sediment.

The critical factor for corals in the above discussions is that coral species can occur across a wide range of habitats and conditions (Fig. 2), but significant alterations in any of these factors can cause stress to corals and, if prolonged or severe, will result in coral death.

Stresses causing damage to coral reefs

Coral reefs are the net result of growth and destructive processes. These processes can be measured over geological time scales of thousands to millions of years, down to the scale of years to centuries in the case of individual coral colonies. The emphasis of this review is on the scale of years to decades – a scale accessible to human comprehension and experience. The emphasis below is on anthropogenic stresses to reefs, with only a cursory discussion of natural stresses.

Three categories of stresses that damage coral reefs are considered:

- *True natural events that damage coral reefs.* These include: major global cycles and meteor strikes; the consequences of tectonic plate movement (volcanoes and earthquakes); tropical storms; periodic extreme weather events and low tides; outbreaks of predators and disease; extreme variations in temperature.
- *Localized (direct) anthropogenic stresses to coral reefs.* These include: increased sedimentation; inorganic and organic pollution; over-exploitation of fisheries, including damaging practices; engineering modification of reefs; military activities.
- *Natural impacts accentuated by anthropogenic activities (indirect).* These are the most difficult to define, and include: temperature variations and extreme weather events exacerbated by Global Climate Change; increased outbreaks of predators and disease due to human disturbance; increases in radiation; possible changes in current patterns and incidences of low tide events.

Natural threats to coral reefs

Reefs are continually affected by natural disturbances, and these shape the communities that develop. In general, reefs do recover from these natural stresses, provided these are neither particularly severe nor frequent (Done 1999). Non-recovery of reefs is frequently associated with chronic anthropogenic influence, as opposed to natural damage (Connell 1997). The major difficulty now is distinguishing those natural events that are being enhanced or induced by anthropogenic activities such as increases in greenhouse gases in the atmosphere. For other stresses, such as earthquakes and meteor strikes, this is not a question.

Geological disturbances

The largest 'natural' threats to coral reefs are massive climatic changes that occur over geological time scales, the last being the glaciation that ended the Pleistocene and resulted in a drop in sea level of >100 m. Sea levels rose during the Holocene and reached their present levels ~6000 years ago, with corals recolonizing many of the previous reef habitats. These are outside the scope of this review, as are meteor strikes, tectonic plate movement, changes in solar activity, and large-scale changes in current patterns. Recent geological events also, e.g. volcanoes and earthquakes, can cause massive but localized damage to coral reefs particularly around the rim of the Pacific and on some islands of the Caribbean such as Montserrat. Undersea volcanoes, however, provide new habitats for coral reef, evident as numerous atolls (Darwin 1842).

Storms and other climatic disturbances

Storms, especially tropical cyclonic storms (hurricanes in the Atlantic, typhoons in the North Pacific, and cyclones elsewhere in coral reef areas) are the greatest determining factor in the structure of coral reefs (Harmelin-Vivien 1994) and are particularly evident outside the belt 7°N to 7°S (Scoffin 1993). These have a major role in structuring reefs (Massel and Done 1993; Rogers 1993; Done 1999).

Inundation by fresh water

Reefs in lagoons and near large land masses are periodically affected by extreme weather events resulting in masses of fresh water and sediments flowing over and damaging coral reefs. An example is the periodic heavy rainfall events that flood Kaneohe Bay, Hawaii, with a frequency of ~20–50 years and result in massive death of corals because of prolonged lowering of salinity (Jokiel *et al.* 1993; Hunter and Evans 1995). However, the amount and speed of water running off the land has probably been altered by the extensive human activities in the catchment.

Exposure during periodic low tides

Corals are often killed by extreme low tides below the predicted lowest astronomical tides (Loya 1976; Fadlallah *et al.* 1995). Exposures lasting hours to days can occur in enclosed waters such as the Red Sea when there is a coincidence of low tides and long periods of strong unidirectional winds.

Outbreaks of predators and disease

The most dramatic examples of these have been the ‘plagues’ of *Acanthaster planci* since the early 1960s. There is dispute as to whether they are truly natural events or are natural occurrences initiated or accentuated by anthropogenic activities, and they were the subject of a recent popular account by a historian (Sapp 1999).

Predictions

Virtually by definition, no changes in coral reef status due to all the above natural impacts are predicted, and the consequences of these remain totally stochastic (Done 1997). Damage by cyclonic storms, however, can be expected to increase with increased sea surface temperatures. Changes will occur at the scale of individual reefs, but nothing will be detectable at large scales.

Localized (direct) anthropogenic stresses to coral reefs

The predominant stresses of increased sedimentation and pollution, and over-exploitation of fisheries resources, have been well discussed in the literature in the past decade, with all these stresses increasing and resulting in predictions of global threats to coral reefs (Wilkinson 1993; Bryant *et al.* 1998). The following brief discussions will emphasize predictions of future impacts from these stresses on coral reefs around the world.

Global population has increased from 2.5 thousand million in 1950 to ~6.0 thousand million in early 1999, and is predicted to increase 8.0 within the next 25 years (World Resources Institute, Anon. 1998). Most of the increases are occurring in tropical countries with coral reefs (Wilkinson 1996). Similarly, global economic activity has more than tripled in the past three decades, and it is predicted to increase at similar rates in the immediate future (Anon. 1998). The documented degradation of coral reefs has coincided with both of these, and in most cases there is a direct causal relation. Future population and economic growth will certainly result in increased sediment loading, organic and inorganic pollution and more exploitation around areas reported in the predictive maps in Bryant *et al*. (1998).

While these threats were causing considerable damage to coral reefs and steadily increasing proportionally with population and economic growth, the 1997–98 massive global coral bleaching event added a new dimension to the problem.

Increased sediment loads

Increased sedimentation resulting from human activities is probably the largest source of damage to coral reefs adjacent to land masses and on shallow continental shelves – the fringing, platform and many of the barrier reefs in Fig. 1 (Dubinsky and Stambler 1997). Sediment loading is not a significant problem for oceanic reefs because catchments are small and any sediment either is rapidly dispersed by ocean currents or settles into oceanic depths, beyond possible resuspension through wave and current action (the outer barrier, bank and atoll reefs in Fig. 1).

Sediments, particularly small clay particles, remain in suspension and stress corals by reducing ambient PAR, by settling on corals and requiring considerable energy expenditure for removal, or sometimes by completely burying corals and other reef biota. In shallow areas, these sediments are continually resuspended by wave and current disturbance. The Reefs at Risk analysis recognized sediment loading as a significant factor in allocating reefs to high- and medium-risk categories (Bryant *et al.* 1998).

Predictions. Clearly, sediment loading will increase on reefs near large land masses with growth in human populations and economies and extensive logging activity. This will result in increased degradation of these reefs, e.g. around South-East and East Asia, South Asia, eastern Africa, the western Pacific, and some reefs of the Caribbean. Oceanic and bank reefs will be largely unaffected.

Organic and inorganic pollution

These also result from increased human activities and will increase as human development increases in the tropics (Dubinsky and Stambler 1997). Such pollution favours the growth of planktonic and large benthic algae and animal competitors of corals, e.g. in Kaneohe Bay, Hawaii (Smith *et al.* 1981; Hunter and Evans 1995), and has been suggested as a stimulus for increased bioerosion of corals, thereby reducing the structural strength of coral reefs (Glynn 1997). The nexus between eutrophication of coral reef waters and coral degradation is sometimes direct, but damage is frequently associated with either naturally low or reduced populations of algae-grazing fishes or echinoids (McCook in press). Not all corals succumb to increases in pollution, and many species appear to thrive in inshore waters, where community nutrition is essentially heterotrophic (Veron 1986).

Predictions. Nutrient enrichment of coral reef waters will continue to increase near human populations or land masses with significant agriculture or deforestation. The greatest impacts are clearly associated with the simultaneous removal of algae-grazers and these effects will increasingly be seen in South-East and East Asia, South Asia, eastern Africa, in lagoons of coral atolls and reefs off populated Pacific islands and around most reefs of the Caribbean. Again, bank reefs and atolls with low populations will not be affected.

Complex organic and heavy metal pollutants

The effect of such pollution on corals and coral reefs is largely unexplored and may result in long-term damage when other forms of activity are eventually controlled, because of the long persistence of pollutants in waters, sediments and soils (Dubinsky and Stambler 1997). Of most concern are those complex organics, such as PCBs, that mimic reproductive hormones (Taylor and Harrison 1999) because there is a potential for long-term reductions in reproduction of key organisms such as fish and corals.

Predictions. As there are no reports of these specific pollutants causing significant damage or collapse of reef systems, it is not feasible to make such predictions now. However, there is a nagging worry that evidence of subtle effects, such as decreased reproduction or decreased resistance to disease of reef animals, may appear when other factors currently damaging reefs are ameliorated. As these pollutants are persistent, cumulative, and can cause changes with minute concentrations, their effects may first be observed on otherwise pristine, remote reefs, but the greatest damage will occur on reefs close to human sources of pollution.

Over-exploitation, especially damaging practices

Damage to reefs has two distinct phases: directly during, and indirectly after, the removal of fish and other resources. The most severe influence is the removal of alga-grazing fishes. For example, the collapse of the coral reefs on the north coast of Jamaica was ultimately caused by over-fishing, but this only became evident after the die-off of grazing urchins (*Diadema antillarum*), combined with two hurricanes (Hughes 1994). Similar collapses of coral reef ecosystems following extreme fishing pressures have been recorded in eastern Africa (McClanahan *et al.* 1996) and in the southern islands of Japan (Chou and Yamazato 1990), where large-scale bioerosion by grazing echinoids was apparent. There is often strong synergism between nutrient enrichment and over-fishing in causing damage to coral reefs (McCook in press).

During fishing, there is often considerable collateral damage caused by anchors, discarded nets, ships running onto reefs etc. But far more serious damage results from the use of deliberately damaging practices: blast (dynamite); muro ami (driving fish into set nets by striking the coral with rocks or sticks); and poison fishing, especially with cyanide (Johannes and Riepen 1995). Initially, the damage from these activities was localized (within a half-day trip from the fisher's home), with large areas of coral reefs (42% in Bryant *et al.* 1998) unaffected. But since the late 1980s, roving bands of fishermen have been systematically targeting reefs in widening concentric circles out from the major importing markets of East Asia (Hong Kong and other ports of China, Japan and Taiwan). The major targets are large grouper, especially *Plectropomus* spp., humphead wrasse (*Cheilinus undulatus*) and other prized fishes for the live-fish restaurant trade. The usual method of extraction is with cyanide, which temporarily stuns the large fish, but kills all small fish and other invertebrates, including the corals (Johannes and Riepen 1995). These activities are additional to the removal of shark (for shark fins), lobster, giant clam, edible holothurians, trochus, pearl shell and specimen molluscs, such that these organisms are now rare on many reefs in the Indo–Pacific region, including reefs previously considered pristine (Hodgson 1999).

Predictions. Fishing pressure will increase and further reduce fish populations on reefs that are already over-exploited; this will result in slow, or sometimes sudden, degradation of coral reefs and shifts away from dominance by corals to dominance by macroalgae. It is also clear that there will be increased exploitation of fisheries on many unprotected coral reefs around the world, with localized extinctions of many prized target fish on reefs around South-East Asia.

Pollution by oil and petroleum products

These attract more media attention than does chronic pollution from domestic, agricultural and industrial wastes, but they rarely cause significant impacts (Brown 1997). The only damage reported results from chronic pollution near oil installations (often reported to be due to associated chemicals and dispersants) such as Eilat (Loya and Rinkevich 1980) and Aruba (Bak 1987), or when oil is trapped in coastal wetlands in the vicinity of reefs and continues to leach out onto reefs, e.g. near the Panama Canal (Jackson *et al.* 1989). Oil spills at sea float away from corals or are shed by coral mucus, thereby causing minimal damage. For example, the massive oil spills resulting from the war adjacent to the Arabian Gulf in 1991 caused minimal damage to the coral reefs (Vogt 1995), although it is acknowledged that these reefs were probably acclimatized to low levels of oil pollution.

Predictions. Chronic oil pollution will continue to cause localized damage around petroleum installations, e.g. in the Middle East and the Panama Canal, but it is unlikely that major oil spills near coral reefs will cause significant damage.

Effects of engineering and military damage

Most of the reefs amongst the 10% reported by Wilkinson (1993) to have been lost were destroyed by engineering activity – building of airports, removal of rock and sand for construction, and blasting to allow port access. Also, some reefs had been blasted during atmospheric and underground nuclear tests. Although reefs used for atmospheric tests have shown recovery of corals away from the direct impact zone, reefs such as Eniwetok are effectively lost because there is too much residual radioactivity for human occupation. The extensive damage to reefs in the Pacific during World War II is no longer evident, except for wrecked ships that have become artificial reefs (Maragos *et al.* 1998).

Predictions. Engineering impacts will increase as populations seek more access to coastal lands and modify them for human habitation and industry. A worrying feature accompanying the boom in reef-based tourism will be the construction of more airports over coral reefs in remote areas, and the building of concrete barriers to protect valuable tourism infrastructure from erosion caused by rising sea levels and increased storm activity. Military damage will remain insignificant, and nuclear testing on coral atolls has ceased.

Global anthropogenic accentuation of natural impacts (indirect)

The major factor proposed behind anthropogenic changes to otherwise natural phenomena is Global Climate Change (GCC) induced by increases in greenhouse gases (H_2O, CO_2, CH_4 and N_2O) in the atmosphere. These have been steadily rising since the industrial age (i.e. 1750) and will reach double those concentrations in 2065, i.e. after 300 years (Kleypas *et al.* 1999), with the greatest rates of change within recent decades. GCC is almost certainly having the following effects: raising sea surface temperatures and sea levels; changing weather patterns (e.g. alteration of frequency and strength of El Niñno–Southern Oscillation events), including greater fluctuation in weather events (storms, floods, droughts); possibly altering current patterns; changing sea-water chemistry with increased CO_2 concentrations; and the associated effect of increasing ultraviolet B (UVB) radiation (Smith and Buddemeier 1992; Wilkinson and Buddemeier 1994). The other factor considered is whether human activities are altering the patterns of occurrence of predators and diseases.

Temperatures and coral bleaching

The massive coral bleaching and mortality in 1997–98 in many parts of the world served as a probable early warning of far more serious impacts in the future as a result of increasing greenhouse gas emissions (Wilkinson *et al.* 1999). It was the most severe of a series of recent bleaching events at near-global scales (1982–83, 1987–88, 1990–91, 1994–95, and 1996) that appear to show increasing severity each time (Williams and Bunkley-Williams 1990; Goreau and Hayes 1994; Hoegh-Guldberg and Salvat 1995). The history of bleaching and threats posed are well discussed in Hoegh-Guldberg (1999).

Predictions. Direct anthropogenic effects can be predicted where human populations exploit or live adjacent to coral reefs, but coral bleaching and the effects of CO_2 changes in sea water (below) will have impacts at truly global scales. It is virtually certain that bleaching and mortality will increase in both frequency and severity as atmospheric and sea surface temperatures rise, and damage to coral reefs will probably be very severe in the next 5 decades, as indicated by Hoegh-Guldberg (1999).

Increasing CO_2 concentrations and coral calcification

Increases in greenhouse gases are inducing another potential major threat to coral reefs, caused by a change in the balances between carbonate and bicarbonate ions in sea water. The changes will probably result in reduced calcification in corals, particularly in higher latitudes, and pose an increasing threat for the future of reefs (Kleypas *et al.* 1999). This is discussed in more detail in Hoegh-Guldberg (1999).

Predictions. There is no evidence of present-day reductions in coral calcification or consequent reductions in coral cover on reefs in the field, but Kleypas *et al.* (1999) and Hoegh-Guldberg (1999) predict a strong likelihood of significant damage to coral reef communities in the future as CO_2 concentrations continue to increase.

Increases in UVB radiation

Coral reefs normally experience high levels of UVB radiation, and many organisms have developed mechanisms to block out the harmful effects of the radiation (Shick *et al.* 1996); although those authors concluded that UVB may have some sublethal effects on coral reefs, an increase in the level of the radiation due to reduction in the ozone barrier is unlikely to have any significant effect on reef communities. The only likely effect will be that coral distribution may shift a few centimetres deeper to compensate for the increased UVB radiation.

Predictions. No significant effects of increased UVB can be anticipated on coral reefs.

Changes in sea level, weather and current patterns

The predicted rise of approximately 0.5 m in sea level within the next century will have virtually no effect on coral reefs, except in a positive sense of providing corals with more room to grow over the large areas of shallow reef flats where aerial exposure at low tide has hitherto prevented coral growth (Buddemeier and Smith 1988; Wilkinson and Buddemeier 1994; Wilkinson 1996).

The same, however, cannot be said for coral sand cays, because there is no apparent mechanism, other than through engineering, that will permit the necessary upward growth of these cays to keep pace with rapidly rising sea levels. Intrusion of sea water into the fresh groundwater will threaten agriculture and supplies of drinking water on many remote islands and probably render them uninhabitable (Wilkinson and Buddemeier 1994; Wilkinson 1996).

Most models of GCC indicate that greater fluctuations in ambient weather are a likely consequence, with more extreme events of rainfall or, alternatively, drought. Certainly, sporadic, severe rainfall events will result in increased sediment flows and localized damage to coral reefs adjacent to large land masses. Similarly drought may also result in increased sedimentation if grazing lands and forests are laid bare of vegetation, permitting small rainfall events to remove topsoil (Wilkinson and Buddemeier 1994; Wilkinson, 1996).

The massive El Niño–La Niña event of 1997–98 was the largest of this type ever recorded and the impacts on the coral reefs were far more serious than any impact on coral reefs in probably thousands of years (Wilkinson 1998; Hoegh-Guldberg 1999; Wilkinson *et al*. 1999). Although it remains speculative whether this event, and the resultant damage, was a direct result of GCC, recent models suggest that the magnitude and frequency of El Niño–Southern Oscillation events will increase (Timmermann *et al.* 1999).

Predictions. No significant impacts on coral reefs are anticipated from a rise in sea level, but this may force the wholesale movement of island populations off low-lying coral cays. Changes in weather patterns will certainly affect coral reefs, but this will be mostly additive to the effects of pollution and sediment flow of direct anthropogenic origin. If more frequent and stronger El Niño–Southern Oscillation events occur, then the consequences for reefs will be as severe as predicted by Hoegh-Guldberg (1999). There has been considerable speculation that GCC may result in major shifts in currents, but such shifts remain far too speculative to put into predictions at the moment.

Overall predictions for the future

Past predictions

There have been four recent 'predictions' on the fate of coral reefs: Wilkinson (1993) and Wilkinson *et al.* (1994); Bryant *et al.* (1998); Hoegh-Guldberg (1999); and Risk (1999). These all emphasize that coral reefs are under immediate and increasing threat with the first two focussing on direct anthropogenic stresses (increases in pollution and sedimentation, and over-exploitation), whereas the third focuses on truly global phenomena associated with GCC.

The predictions in Wilkinson (1993) were based on an estimation that 10% of the world's reefs were already irreparably damaged. He predicted that a further 30% would be similarly degraded in 10–20 years (2002–12), and a further 30% were predicted to go the same way in 20–40 years (2012–32), with a caveat that effective management could reverse this trend. These predictions were based almost entirely on projections regarding human populations in the tropics and increasing economic development, which would lead to an increase in widespread, but localized, direct anthropogenic stresses. The true global impacts of GCC were virtually discounted. The predictions over-estimated the extent of localized anthropogenic stresses, because they ignored large areas of submerged bank reefs in oceanic waters that would be remote from these stresses, e.g.: Chagos and Mascarene plateaux in the Indian Ocean; deep reefs in the South China Sea and across the Pacific; and Flower Gardens and Campeche Banks in the Caribbean. Nevertheless, these estimations were widely reported and entered into the 'folklore' of conservation efforts on coral reefs and served as an alarm call.

A subset of the above predictions suggested that 11% of the reefs in South-East Asia were already degraded, 48% were under immediate threat, and 36% under slightly longer-term threat of severe degradation (Wilkinson *et al.* 1994).

Similar conclusions about anthropogenic impacts were drawn by a global task team in 1994, with a minimalist statement about GCC: 'Climate change by itself is unlikely to eliminate coral reefs, but climate change will create hardships for people dependent on these reefs, because of changes in reef structure, function, distribution and diversity' (Wilkinson and Buddemeier 1994).

Although Bryant *et al.* (1998) did not make specific predictions on the temporal future for coral reefs, their estimations of the risks facing the existing reefs provide the basis for predictions. This was a map-based assessment of those reefs at, or potentially at, risk from human activities and the conclusions were that 58% of the world's reefs were under either 'high' or 'medium' risk of degradation from direct anthropogenic stresses. These risks were greatest in South-East Asia and least in the Pacific (82% compared with 41% at 'high' or 'medium' risk). These assessments are similar to those made earlier (Wilkinson 1993; Wilkinson *et al.* 1994), which were based on the original area of reefs (including ~10% lost during human development).

Present predictions

The most recent predictions are focussed on the severe bleaching event of 1997–98 and four runs from three mathematical models of GCC that correlate with recent history. These paint a bleak picture of the future for coral reefs for the next century (Hoegh-Guldberg 1999). Continued unrestricted releases of CO_2 will result in two increasing threats to coral reefs: more frequent and severe bouts of coral bleaching and mortality, associated with El Niño events; and balances of dissolved CO_2 that will be increasingly unfavourable for calcification by corals and coralline algae. The predictions are that rises in sea surface temperature within the next 20 years will bring normal temperatures into the range experienced during the 1997–98 bleaching event and regular bouts of higher temperatures will impede recovery processes, which normally require 10–30 years. Thus, in 20–30 years (2019–29), all bleaching events will be comparable to the 1998 event, but will occur almost every year. Reefs like the Great Barrier Reef will then become dominated by faster-growing macroalgae at the expense of corals by 2050. If GCC continues, Hoegh-Guldberg (1999) predicts the complete loss of coral reefs over global scales. These predictions can be obviated only if either there are significant reductions in the releases of CO_2 by both developed and developing countries, or there is major sequestration of CO_2 as indicated by Hunter (1999).

Some aspects of the predictions by Hoegh-Guldberg (1999) warrant re-evaluation. The suggestion that the protective function of the Great Barrier Reef may be lost within several decades is unlikely, as it would probably require centuries before there was sufficient erosion of the base limestone structure to affect the coast.

The first recommendation of Risk (1999) is that existing coral reef monitoring programmes be abandoned. This would negate considerable current scientific activity that seeks to repeat previous monitoring to detect long-term changes in coral reefs. Much of our understanding of coral reef ecology and dynamics derives from repetition of a variety of monitoring programmes (e.g. Hughes 1994; Connell 1997; Done 1997). Most scientists do indeed adhere to the precautionary principle (Risk's third recommendation); however, reef users and governments in developing countries face urgent problems of feeding and housing expanding populations and are often unable to commit to long-term planning for reef conservation (Wilkinson 1996).

Risk's (1999) second prediction on 'an effective system of monitoring for stress' will be difficult to assess. Many developing countries have excellent legislation to protect marine environments, especially Marine Protected Areas, but the sad fact is that >90% of MPAs have little or no effective management, i.e. the legislation is ignored (Kelleher *et al.* 1995). Even fewer contries have consistent and extensive reef-monitoring programmes. The monitoring programmes for Australia were developed during extensive discussions between scientists and resource managers, and are now the basis for management of areas such as the Great Barrier Reef. Management decisions are made under strong existing legislation using results from monitoring, but these are not the only criteria, and many social and economic factors are also involved.

Risk (1999) suggests that 'reefs as some of us knew them will have vanished from much of the inhabited coastlines'. But those reefs themselves were the product of change from even earlier reefs; reefs are dynamic structures subject to continual change from natural as well as anthropogenic impacts (Done 1999). Coral reefs close to habitation will suffer changes such as reduction in target fish species, some enhanced eutrophication, physical damage from anchors, bleaching etc., and some reefs will be degraded and disappear. However, a large proportion will continue to function as coral reefs.

The 'threshold' effect

Recent research and discussion on coral reefs has introduced the notion of critical thresholds, by which a reef appears to sustain little damage and change in the face of increasing levels of chronic stress, until a critical point is reached when the reef effectively collapses and there is a total switch in community structure. One example cited by Knowlton (1998) for this was the reef on the north coast of Jamaica that persisted for decades with virtually no populations of fishes, until a series of unrelated events caused system collapse with no significant recovery, nearly two decades later (Hughes 1994). Other examples are cited by Done (1999), with changes in dominance of reefs by corals to essentially algal reefs following critical disturbances. This threshold concept renders the task of predicting the future of coral reefs particularly difficult, because if it holds true, then reef systems may effectively collapse following virtually no visible warnings of change.

The 'buffering' effect

The present climate-related stresses facing coral reefs will have reduced impacts on large complex ecosystems like the Great Barrier Reef and Indonesia because they contain large populations of many species growing in a wide range of habitats. Thus, effects in one part of these systems can be buffered by other unaffected areas, or from areas where corals are acclimatized to temperature variation, e.g. inshore or lagoon areas which experience wider ranges of temperature naturally (e.g. the example in Palau above; Paulay, Richmond and Birkeland, personal communication). Such areas will probably provide a continual supply of more resistant larvae to repopulate depleted areas. Thus, the predictions of Hoegh-Guldberg (1999) should be regarded with caution for large buffered ecosystems. By contrast, small, isolated, uniform reef habitats are likely to suffer greater impacts because there are no readily identifiable sources of more stress-resistant larvae.

Questions for the future

The following are a series of frequently asked questions that arise as a result of the increasing anthropogenic damage to coral reefs, and particularly examples like the 1997–98 mass bleaching event.

How rapidly will recovery occur after the 1997–98 bleaching? As stated above, reefs will recover within 10–30 years to fully functional systems, provided that there are adequate sources of larvae and that conditions are favourable. Where reefs have been severely damaged, few adult corals survive, with most being slow-growing massive species (e.g. *Porites*); thus, the supply of larvae will be very limited and coral diversity will be markedly lower. Recovery will be longer, i.e. 50 years or more. Moreover, recovery will be slowed if fish populations are low, or if pollution and sedimentation are high as a result of direct anthropogenic disturbance. Therefore, greater attention must be paid to managing direct anthropogenic stresses to reefs.

And what happens if similar bleaching occurs again (and again)? Another bout of bleaching within the 10–30-year recovery period will probably lower coral diversity by limiting recovery of some of the remaining slow-growing corals. If bleaching becomes very frequent, as Hoegh-Guldberg (1999) predicts, then diversity will drop dramatically, with only a few resistant species present on each reef. Algae will dominate the reefs, which will lose structural complexity, in turn reducing habitat for fishes and other reef animals.

Will corals adapt by growing in deeper, cooler water? This is unlikely as corals are light dependent and are particularly restricted during winter, with low angles of incident sunlight reducing penetration of light (PAR) to deeper water. Moreover, the 1997–88 bleaching event affected corals down to depths of 30 m and deeper (Wilkinson 1998).

Will coral reefs move into higher latitudes? Again, this is unlikely because reduced light energy in winter and the enhanced effects of increased acidity of sea water due to increases in CO_2 concentration will be greatest in higher latitudes (Kleypas *et al.* 1999).

Will corals evolve to the new warmer environment? Eventually yes, but not within the next few centuries to millennia. There is the possibility that there may be a change in the symbiosis between corals and zooxanthellae, with corals becoming host to more-temperature-resistant species of dinoflagellates, as suggested by Buddemeier and Fautin (1993). But the likely consequence if GCC continues to increase will be a massive reduction in species diversity on coral reefs and a similar reduction in coral accretion rates.

Will corals become extinct? No, but there may be massive losses of species similar to the mass extinctions in past geological history. Corals will eventually bounce back and evolve to again form massive coral reefs, which will resemble the present reefs, but with a markedly different species structure. Coral taxonomy books will have to be rewritten.

Conclusions

The increasing rate of direct anthropogenic damage will cause further degradation to the major coral reef areas of South-East Asia (Indonesia, Philippines, Malaysia, Thailand and Vietnam), South Asia (India and Sri Lanka), eastern Africa (Madagascar, Mozambique, Kenya and Tanzania), and many parts of the central and southern Caribbean, especially around the larger islands and along the coasts of Central and South America. There are few encouraging signs on the horizon for these areas, because the rate of degradation due to population growth is outstripping the substantial efforts at integrated coastal management. For example, the combined populations of Indonesia and the Philippines are predicted to increase by over 100 million by 2025 (Anon. 1998). Some significant successes will be recorded, but there will be scenes of desolation all around the success stories.

What is of critical concern is whether direct and indirect human activities are pushing reefs beyond their ecological potential for rapid recovery. There is little doubt that coral reefs will eventually recover from the present ranges of human-induced pressures and continue to exist and evolve in changing environments into the future. On past evidence, they should outlive the species causing most damage at the moment, *Homo sapiens*. The time frame for these recoveries may be of the order of hundreds to thousands of years, possibly extending to hundreds of thousands or millions of years. The major immediate concern, however, is that many human societies have developed a strong dependence on coral reefs and their productivity, and these peoples will be badly affected if reefs are seriously damaged (Wilkinson 1996; Wilkinson *et al.* 1999). However, what humans are doing to the climate may have far more severe impacts on terrestrial ecosystems and thereby threaten the survival of the human species, along with many others on this planet.

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